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FOLIAR MICROMORPHOLOGY OF MEXICAN OAKS (*QUERCUS*: FAGACEAE)

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ABSTRACT

Mexico is the main center of diversity of the genus *Quercus* in the Western Hemisphere. Despite recent advances in the knowledge of Mexican oaks, a degree of taxonomic confusion still remains, mainly within particular species complexes. In this study, scanning electron microscopy was used to describe micromorphological foliar structures (trichomes, epicuticular waxes and stomata) from the abaxial and adaxial leaf surfaces of Mexican oak species, with the main goal of assessing the taxonomical utility of these characters. In total, 27 species belonging to sections *Quercus* (white oaks) and *Lobatae* (red/black oaks) were examined, particularly focusing on several groups of closely related species with problematic taxonomic delimitation and on species that are known to hybridize. Several trichome types were observed, including both glandular (simple and bulbous) and eglandular (solitary, multiradiate, stellate, fused stellate and fasciculate stipitate). Epicuticular waxes were structured as films, grooved films, crusts, granules, platelets and platelets arranged in rosettes. Stomata were elliptical and raised above or leveled with the foliar surface. Among the three types of structures examined, trichomes appeared to be the most useful for taxonomical purposes, followed by epicuticular waxes. All species had different combinations of character states for these micromorphological structures, which permitted the elaboration of keys to identify species within the problematic groups.

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Key words: epicuticular waxes, foliar trichomes, *Quercus*, stomata, taxonomy.

RESUMEN

México es el principal centro de diversidad del género *Quercus* en el Hemisferio Occidental. A pesar de los avances recientes en el conocimiento de los encinos mexicanos, aún existe cierto grado de confusión taxonómica, particularmente dentro de algunos complejos de especies. En este estudio se utilizó microscopía electrónica de barrido para describir las estructuras micromorfológicas foliares (tricomas, ceras epicuticulares y estomas) de ambas superficies foliares (haz y envés) en representantes seleccionados de encinos mexicanos, con el objetivo de evaluar la utilidad taxonómica de estos caracteres. En total se examinaron 27 especies, pertenecientes a las secciones *Quercus* (encinos blancos) y *Lobatae* (encinos rojos y negros), incluyendo varios grupos de plantas cercanamente relacionadas con problemas de delimitación taxonómica, así como especies que presentan hibridación. Se encontraron varios tipos de tricomas, tanto los de tipo glandular (simples y bulbosos) como los no glandulares (solitarios, multirradiados, estrellados, estrellados fusionados y fasciculado estipitados). Las ceras epicuticulares se observaron en forma de capas, capas fisuradas, costras, gránulos, placas y placas en rosetas. Los estomas fueron elípticos y se encontraron elevados con respecto a la superficie foliar o al mismo nivel que ésta. Entre los tres tipos de estructuras examinadas, los tricomas fueron los más útiles para propósitos taxonómicos, seguidos por las ceras epicuticulares. Todas las especies tuvieron diferentes combinaciones de estados de carácter para estas estructuras micromorfológicas, lo que permitió la elaboración de claves para identificar a las especies dentro de los grupos problemáticos.

Palabras clave: ceras epicuticulares, estomas, *Quercus*, taxonomía, tricomas foliares.

INTRODUCTION

Micromorphological structures of plant leaf surfaces, such as trichomes, epicuticular waxes and stomata, can be observed in detail through scanning electron microscopy (SEM), and often provide additional taxonomic information (Eglinton and Hamilton, 1967; Engel and Barthlott, 1988; Haron and Moore, 1996; Neinhuis and Barthlott, 1997; Stockey and Frevel, 1997). The genus *Quercus* (the oaks) is characterized by complicated taxonomical patterns (Manos et al., 1999), resulting

from frequent parallel or convergent evolution of vegetative characters, pronounced intraspecific variation, low differentiation among closely related species, and hybridization (Tucker, 1974; Hardin, 1975; Aas, 1993; Kleinschmit et al., 1995; Bruschi et al., 2000; Kremer et al., 2002; Bruschi et al., 2003; González-Rodríguez et al., 2004; Tovar-Sánchez and Oyama, 2004; González-Rodríguez and Oyama, 2005). In this plant group, the characterization of micromorphological structures of the foliar surfaces can significantly contribute to the recognition and correct identification of species and natural hybrids, as has been shown in several studies (Hardin, 1975, 1979a, b; Manos, 1993; Llamas et al., 1995; Bussotti and Grossoni, 1997; Valencia and Delgado, 2003).

In Mexico, the three sections of genus *Quercus* subgenus *Quercus* are well-represented (Nixon, 1993). These sections are *Quercus* (white oaks, with 81 species and 47 endemics), section *Lobatae* (red oaks, with 76 species and 61 endemics), and section *Protobalanus* (intermediate or golden cup oaks, with four species, one endemic) (Valencia, 2004). Most of the species are found in the temperate mountainous regions of the country, forming forests and woodlands often in association with pines, although some oaks are also present in tropical forests and cloud forests, and others in arid areas (Nixon, 1993; Rzedowski, 1994; Valencia, 2004). Despite several recent studies on the taxonomy of Mexican oaks, some of which have included the examination of micromorphological features (Spellenberg, 1992; Nixon, 1993; Spellenberg and Bacon, 1996; Romero et al., 2002; Valencia and Delgado, 2003; Valencia, 2004; Vázquez et al., 2004), a great deal of effort is still necessary to understand relationships among species and groups of species in this geographical area (Nixon, 1993).

The main aim of this work was to contribute a detailed SEM characterization of stomata, epicuticular waxes and trichomes of the adaxial and abaxial foliar surfaces for a sample of Mexican white and red oak species, that may be useful for taxonomic purposes. We also discuss these results in comparison with previous reports and generalizations on North American and European species.

MATERIAL AND METHODS

Analyses using scanning electron microscopy (SEM) were performed on mature leaves of 27 taxa of the genus *Quercus* sampled in 11 states of Mexico (Table 1). Of these, 9 taxa were white oaks (section *Quercus)* and 18 taxa were red oaks (section *Lobatae*), encompassing various degrees of relatedness. Several

Table 1. List of taxa sampled for this study and state and locality of collection.

Taxa	State of collection	Locality	Lat N / Long W	Voucher
Section *Quercus*				
Q. arizonica	Durango	Tepehuanes	25°20' / 105°43'	*C. Scareli 1* (private collection)
Q. deserticola	Michoacán	Capula	19°28' / 101°30'	*C. Scareli 19* (IEB)
Q. glaucoides	Oaxaca	Ixtlán	17°19' / 96°29'	*C. Scareli 2* (IEB)
Q. liebmannii	Guerrero	Along highway 93, Tixtla de Guerrero	17°34' / 99°23'	*C. Scareli 3* (IEB)
Q. magnoliifolia	Guerrero	Cerro Huizteco, Taxco de Alarcón	18°35' / 99°35'	*C. Scareli 4* (IEB)
Q. oleoides	Oaxaca	Ixtlán	17°19' / 96°29'	*C. Scareli 5* (IEB)
Q. peduncularis	Chiapas	San Cristóbal de las Casas	16°44' / 92°38'	*C. Scareli 6* (IEB)
Q. resinosa	Michoacán	San Miguel del Monte	19°36' / 101°07'	*C. Scareli 7* (IEB)
Q. rugosa	Michoacán	Along highway 15, Zacapu	19°49' / 101°47'	*C. Scareli 8* (IEB)
Section *Lobatae*				
Q. acutifolia	Guerrero	Cerro Huizteco, Taxco de Alarcón	18°35' / 99°35'	*C. Scareli 9* (IEB)
Q. affinis	Puebla	Zacatlán	19°56' / 97°57'	*C. Scareli 10* (IEB)
Q. castanea	Morelos	Huitzilac	19°01' / 99°16'	*C. Scareli 11* (IEB)
Q. coccolobifolia	Sonora	Yecora	28°22' / 108°56'	*C. Scareli 12* (IEB)
Q. conspersa	Guerrero	Along highway 93, Tixtla de Guerrero	17°34' / 99°23'	*C. Scareli 13* (IEB)
Q. conzattii	Durango	La Michilia	23°19' / 104°11'	*C. Scareli 14* (IEB)
Q. crassifolia	Michoacán	Santa Clara del Cobre	19°24' / 101°38'	*C. Scareli 15* (IEB)
Q. crassipes	Michoacán	Santa Clara del Cobre	19°24' / 101°38'	*C. Scareli 17* (IEB)
Q. crispipilis	Chiapas	Along highway 199, Ocosingo	16°57' / 92°06'	*C. Scareli 18* (private collection)
Q. x *dysophylla*	Michoacán	Santa Clara del Cobre	19°24' / 101°38'	*C. Scareli 20* (IEB)
Q. eduardii	Durango	La Ferrería	23°56' / 104°42'	*C. Scareli 21* (IEB)
Q. fulva	Sinaloa	Loberas	23°30' / 105°50'	*C. Scareli 22* (private collection)
Q. laurina	Michoacán	Santa Clara del Cobre	19°24' / 101°38'	*C. Scareli 23* (IEB)
Q. ocoteifolia	Chiapas	San Cristóbal de las Casas	16°44' / 92°38'	*C. Scareli 24* (IEB)

Table 1. Continuation.

Taxa	State of collection	Locality	Lat N / Long W	Voucher
Q. radiata	Durango	Tepehuanes	25°20' / 105°43'	*C. Scareli 25* (IEB)
Q. scytophylla	Guerrero	Along highway 93, Tixtla de Guerrero	17°34' / 99°23'	*C. Scareli 26* (IEB)
Q. urbanii	Guerrero	Cerro Huizteco, Taxco de Alarcón	18°35' / 99°35'	*C. Scareli 27* (IEB)
Q. viminea	Jalisco	Chimaltitlán/Los Huicholes	21°46' / 103°46'	*C. Scareli 28* (IEB)

groups of closely related species with problematic taxonomic delimitation were included, as well as species that are known to hybridize. For example, *Q. affinis* and *Q. laurina* are morphologically distinguishable but intergrade within an area of probable secondary contact and hybridization (González-Rodríguez et al., 2004), and are also related to *Q. ocoteifolia* (Valencia, 1994). *Quercus conzattii*, *Q. radiata* and *Q. urbanii* were included by Spellenberg and Bacon (1996) in subsection *Racemiflorae* of the red oaks, and have similar leaf morphologies. The first one of these species hybridizes with *Q. eduardii*, a phenotypically very different oak (Bacon and Spellenberg, 1996). The taxon named *Q.* x *dysophylla* is a hybrid between *Q. crassipes* and *Q. crassifolia*, also two distantly related species (Tovar-Sánchez and Oyama, 2004). Other groups difficult to delimit and/or hybridizing species included in this study were *Q. acutifolia* and *Q. conspersa* (Romero et al., 2000), *Q. liebmannii*, *Q. magnoliifolia*, *Q. peduncularis* and *Q. resinosa*, and *Q. coccolobifolia* and *Q. viminea* (Table 1).

Leaves used for SEM analysis were collected, stored in paper bags, and dried at room temperature in a shaded place. A pressed specimen was also prepared for each tree sampled, and the taxonomic identification of the material was performed at the National Herbarium of Mexico (MEXU). Vouchers were deposited at the Herbarium IEB, Centro Regional del Bajío, Instituto de Ecología, A.C. (Table 1). In total, four individuals per species and three leaves per individual were analyzed. Samples to be observed with SEM were prepared by removing approximately 24 mm^2 from the internerval zone of each leaf. The samples were affixed to aluminium stubs with carbon conductive adhesive tape and gold coated (Bal-Tec SCD 050 sputter-coater). Observations were performed using a scanning electron microscope Jeol (5610LV) at an accelerating voltage of 15 KV (Hayat, 1983). The nomenclature

proposed by Barthlott et al. (1998) was followed for the description of epicuticular waxes, and the guides of Hardin (1979a) and Theobald et al. (1979) were used for the classification of trichomes.

Several studies of micromorphological structures in oaks have concentrated only on the abaxial leaf surface (e.g. Bussotti and Grossoni, 1997; Valencia and Delgado, 2003), because it usually has a greater diversity of trichome types and therefore provides more characters for identification (Hardin, 1979b; Llamas et al., 1995). In this study, however, both the abaxial and adaxial leaf surfaces of the species were analyzed, as recommended by Hardin (1979b), because the quantitative and qualitative differences among the two surfaces may be a source of additional information.

For each species, the maximum, minimum and mean number and length of trichome rays were obtained for the different types of trichomes present on both the abaxial and adaxial leaf surfaces. For a few species it was not possible to obtain some of these data because of problems with the preparation of the samples.

RESULTS

There was variation in epicuticular waxes, types of trichomes, and position of stomata with respect to leaf surface among the 27 sampled *Quercus* species (Tables 2 and 3). The types of trichomes observed were glandular (simple and bulbous) and eglandular (solitary, stellate, fused stellate, multiradiate, fasciculate and fasciculate stipitate). There were also differences in the number of rays and ray length among the studied species. In general, multiradiate, fasciculate stipitate and stellate trichomes had more and longer rays than other trichome types. In contrast, the simple glandular trichomes were comparatively shorter, but there were some exceptions, for example on the abaxial leaf surfaces of *Q. conzattii*, *Q.* x *dysophylla*, *Q. fulva*, *Q. rugosa* and *Q. viminea*, and on the adaxial leaf surfaces of *Q. eduardii* and *Q. laurina* (see the following description of each species).

The types of epicuticular waxes were films, grooved films, crusts, granules, platelets and platelets arranged in rosettes. The most frequent types observed on the abaxial surface were films (44.4%), followed by platelets (29.6%), whereas the adaxial surface was more diverse in the types of waxes present; the most frequent were crusts (48.2%), films (25.9%) and platelets arranged in rosettes (14.8%). Grooved film was the least frequent type on both the adaxial and abaxial surfaces (3.7%).

The shape of stomata was elliptical in all species analyzed. Nevertheless, there were differences in the position of stomata with respect to leaf surface, and in

Table 2. Types of trichomes present on leaves of 27 Mexican *Quercus* species. Adaxial surface / abaxial surface. + = present, - = absent.

Taxon	Trichome types							
	Simple	Bulbous	Solitary	Multiradiate	Stellate	Fused stellate	Fasciculate stipitate	Fasciculate
Section *Quercus*								
Q. arizonica	-/-	-/-	-/-	-/-	-/-	+/+	-/-	-/-
Q. deserticola	+/+	-/-	-/-	-/-	-/-	-/-	-/+	+/-
Q. glaucoides	-/+	-/-	-/-	-/-	-/-	-/-	-/+	-/-
Q. liebmannii	+/+	-/-	-/-	-/-	-/+	-/+	-/+	-/-
Q. magnoliifolia	-/+	-/-	-/-	-/-	-/-	-/+	-/-	-/-
Q. oleoides	-/-	-/-	-/-	-/-	-/-	-/+	-/-	-/-
Q. peduncularis	-/+	-/-	-/-	-/-	-/-	-/-	-/+	-/+
Q. resinosa	-/+	-/-	-/-	+/-	+/-	-/+	-/+	-/-
Q. rugosa	-/+	-/-	-/-	-/-	-/-	-/-	+/+	-/+
Section *Lobatae*								
Q. acutifolia	-/+	-/-	-/+	-/+	-/+	-/-	-/-	-/-
Q. affinis	+/+	-/-	-/-	+/-	-/-	-/-	-/+	-/-
Q. castanea	-/+	-/-	-/-	-/-	-/-	-/-	-/+	+/+
Q. coccolobifolia	-/+	-/-	-/-	-/-	-/-	-/-	-/+	-/-
Q. conspersa	-/+	-/-	-/-	-/-	-/+	-/-	-/-	-/-
Q. conzattii	+/+	-/-	-/-	+/-	-/+	-/-	-/+	-/-
Q. crassifolia	+/+	-/-	-/-	-/-	-/-	-/-	-/+	-/-
Q. crassipes	-/+	-/-	-/-	-/+	-/-	-/-	-/+	-/-
Q. crispipilis	-/-	-/-	-/-	+/-	-/-	-/-	-/+	-/-
Q. x *dysophylla*	-/+	-/-	-/-	+/-	-/+	-/-	-/+	-/-
Q. eduardii	+/+	-/-	-/-	-/+	-/+	-/-	-/-	-/-
Q. fulva	-/+	-/-	-/-	+/+	-/-	-/-	-/-	-/-
Q. laurina	-/+	-/-	-/-	-/+	-/-	-/-	+/+	-/-
Q. ocoteifolia	+/+	-/-	-/-	-/-	+/+	-/-	-/-	-/-
Q. radiata	-/+	-/-	-/-	+/+	-/-	-/-	-/-	-/+
Q. scytophylla	-/-	-/-	-/-	-/+	-/-	-/-	-/-	-/-
Q. urbanii	+/+	-/-	-/-	-/-	-/-	+/-	-/+	-/-
Q. viminea	+/+	-/+	-/-	+/-	-/+	-/-	-/-	-/-

Table 3. Types of epicuticular wax present on leaves of 27 Mexican *Quercus* species. Adaxial surface / abaxial surface. + = present, - = absent.

Taxon	Epicuticular wax					
	Film	Grooved film	Crusts	Granules	Platelets	Platelets in rosettes
Section *Quercus*						
Q. arizonica	-/-	-/-	+/-	-/-	-/+	-/-
Q. deserticola	-/-	-/-	-/-	-/-	-/+	+ /-
Q. glaucoides	-/-	-/-	-/-	-/-	-/+	+/-
Q. liebmannii	-/+	-/-	+/-	-/-	-/-	-/-
Q. magnoliifolia	-/+	+/-	-/-	-/-	-/-	-/-
Q. oleoides	-/+	-/-	-/-	+/-	-/-	-/-
Q. peduncularis	-/-	-/-	-/-	-/-	-/+	+/-
Q. resinosa	+/-	-/-	-/-	-/+	-/-	-/-
Q. rugosa	-/-	-/-	-/-	-/-	-/+	+/-
Section *Lobatae*						
Q. acutifolia	+/-	-/-	+/+	-/+	+/+	-/-
Q. affinis	-/-	-/+	-/-	-/+	+/-	-/-
Q. castanea	-/-	-/-	+/-	-/-	+/+	-/-
Q. coccolobifolia	-/-	-/-	-/-	-/-	+/+	-/-
Q. conspersa	-/-	-/-	+/-	+/+	-/-	-/-
Q. conzattii	-/-	-/-	+/+	-/-	-/-	-/-
Q. crassifolia	-/+	-/-	+/-	-/-	-/-	-/-
Q. crassipes	-/+	-/-	+/-	-/-	+/-	-/-
Q. crispipilis	-/+	-/-	+/-	-/-	-/-	-/-
Q. x *dysophylla*	+/+	-/-	-/-	-/-	-/-	-/-
Q. eduardii	+/+	-/-	-/-	-/-	-/-	-/-
Q. fulva	-/+	-/-	+/-	-/-	-/-	-/-
Q. laurina	+/+	-/-	-/-	-/-	-/-	-/-
Q. ocoteifolia	+/+	-/-	-/-	-/-	-/-	-/-
Q. radiata	-/-	-/-	+/+	-/-	-/-	-/-
Q. scytophylla	-/-	-/-	+/+	-/-	-/-	-/-
Q. urbanii	-/-	-/-	+/+	-/-	-/-	-/-
Q. viminea	+/+	-/-	-/-	-/-	-/-	-/-

the types of waxes that cover the stomatic structure. The stomata were raised in 63% of the species, leveled with the leaf surface in 29.6%, and both raised and leveled in 7.4% of the studied oaks. In some of the species, the waxes that cover the stomata were different from the wax present on the leaf surface. However, these characters provided comparatively less taxonomic information than trichomes and waxes covering the leaf surface. In the next section, we present the foliar micromorphological descriptions of the *Quercus* species analyzed, grouped according to the two infrageneric sections represented in this study, *Quercus* (white oaks) and *Lobatae* (red oaks).

Subgenus *Quercus*, section *Quercus*

***Q. arizonica* Sarg.** Epicuticular waxes are platelets on the abaxial surface and crusts on the adaxial surface. The stomata are raised and covered by wax platelets (Fig. 1). On the abaxial surface there are fused stellate trichomes, with 10 rays (391-565 μm), covered by grooved wax film, and on the adaxial surface there are fused stellate trichomes, with 5-9 rays (168-365 μm), covered with wax crusts.

***Q. deserticola* Trel.** Leaves with wax platelets on the abaxial surface (Fig. 3) and platelets arranged in rosettes on the adaxial side. The stomata are raised and covered with wax platelets. There are simple (52 μm) and fasciculate stipitate trichomes (4-6 arms, 231-423 μm) on the abaxial surface (Figs. 2 and 3), and simple (38 μm) and fasciculate trichomes (3-5 arms, 227-353 μm) on the adaxial surface. All trichome types observed are covered with wax film.

***Q. glaucoides* M.Martens et Galeotti.** The adaxial surface has epicuticular platelets of wax arranged in rosettes (Fig. 4), and the abaxial surface has platelets. The stomata are raised, with wax platelets. Two types of trichomes are present on the abaxial surface, simple and fasciculate stipitate. Simple trichomes are short (50-94 μm) and are covered in their apical and median region by wax film and in their base by wax arranged in platelets. Fasciculate stipitate trichomes have 6 arms (282-323 μm), and are covered by wax film.

***Q. liebmannii* Oerst.** The epicuticular waxes are films on the abaxial surface and crusts on the adaxial surface (Fig. 5). The stomata are raised, with wax film. On the abaxial surface there are four types of trichomes: stellate trichomes, with 8-10 rays about 165-169 μm long, fused stellate trichomes (with 8-10 arms), fasciculate

stipitate with 6-7 rays (109-200 μm), and simple trichomes (53μm). On the adaxial surface there are only simple trichomes about 112 μm long. All trichomes were covered with wax film, except simple trichomes, that were covered with grooved film.

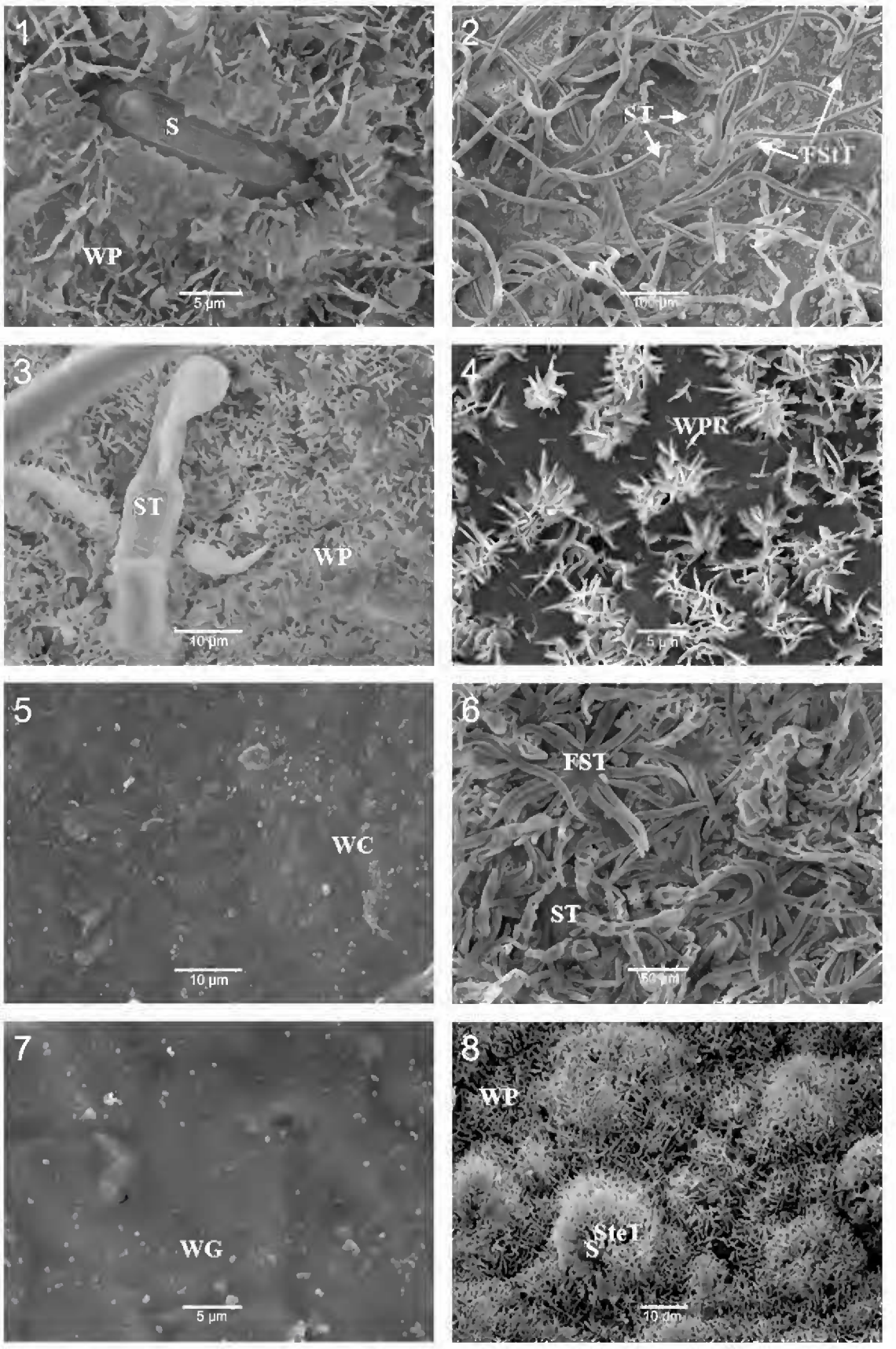
***Q. magnoliifolia* Née.** Epicuticular wax film is present on the abaxial surface and grooved wax film on the adaxial surface. The stomata are situated at the same level of the leaf surface and covered by wax film. Simple trichomes about 15-108 μm long, and fused stellate trichomes with 7-16 rays (76-112 μm), are present on the abaxial surface (Fig. 6), both types covered with grooved wax film. Trichomes were not observed on the adaxial surface.

***Q. oleoides* Schltdl. et Cham.** Epicuticular wax film is present on the abaxial surface and wax granules on the adaxial surface (Fig. 7). The stomata are raised and with wax crusts. There are fused stellate trichomes, with 13 short rays (57-93 μm) on the abaxial surface, covered with wax film. Trichomes are absent from the adaxial surface.

***Q. peduncularis* Née.** On the abaxial surface waxes are structured in platelets (Fig. 8), and in platelets arranged in rosettes on the adaxial surface. The stomata are raised above the epidermis and covered by wax platelets (Fig. 8). Simple trichomes (56 μm), fasciculate trichomes with 2-3 long arms (429-607 μm), and fasciculate stipitate trichomes with 5 arms (478 μm), are present on the abaxial surface. The types of waxes covering the trichomes are crusts in the case of fasciculate trichomes and grooved wax film in fasciculate stipitate trichomes. Simple trichomes are covered by wax film on their apical and median portions and by platelets on the base. The adaxial surface is glabrous.

***Q. resinosa* Liebm.** Waxes arranged in granules are present on the abaxial surface (Fig. 9) and there are wax films on the adaxial surface. The stomata are raised and covered with wax film (Fig. 9). On the abaxial surface there are simple trichomes (70-87 μm), fused stellate trichomes with 9-15 rays measuring 104-208 μm, and fasciculate stipitate trichomes with 4-5 arms about 229-292 μm long, while the adaxial surface has stellate trichomes with 8-11 rays (66-198 μm) (Fig. 10), and multiradiate trichomes, with 8 rays (87-106 μm). All trichome types are covered by wax film, except multiradiate trichomes, that show fissured wax films.

***Q. rugosa* Née.** The types of waxes present are platelets on the abaxial surface and platelets arranged in rosettes on the adaxial surface. The stomata are raised and cov-



Figs. 1-8. (FST = fused stellate trichomes, FStT = fasciculate stipitate trichomes, S = stomata, ST = simple trichomes, SteT = stellate trichomes, WC = epicuticular wax crust, WG = epicuticular wax granules, WP = epicuticular wax platelets, WPR = epicuticular wax platelets arranged in rosettes). Fig. 1. *Quercus arizonica* Sarg. (abaxial surface). Figs. 2, 3. *Quercus deserticola* Trel. (abaxial surface). Fig. 4. *Quercus glaucoides* M.Martens et Galeotti (adaxial surface). Fig. 5. *Quercus liebmannii* Oerst. (adaxial surface). Fig. 6. *Quercus magnoliifolia* Née (abaxial surface). Fig. 7. *Quercus oleoides* Schltdl. et Cham. (adaxial surface). Fig. 8. *Quercus peduncularis* Née (abaxial surface).

ered with wax platelets. The trichomes on the abaxial surface are simple (161-238 μm), fasciculate with 2-3 long rays (527-818 μm), and fasciculate stipitate with 3-5 rays (316-368 μm). On the adaxial surface trichomes are fasciculate stipitate with 4-5 rays 25-403 μm long. All trichome types are covered with fissured wax film.

Subgenus *Quercus,* section *Lobatae*

Q. acutifolia **Née.** On the abaxial surface epicuticular waxes are arranged in granules and in platelets transitional to crusts, the adaxial surface is covered mainly by wax film, but with a few platelets and crusts. The stomata are leveled with the leaf surface, covered by wax crusts. The trichomes on the abaxial surface (Fig. 11) are simple (11-87 μm), multiradiate with 9 short arms (50-62 μm), stellate with 5-6 arms measuring 97-335 μm and solitary (71 μm), all covered by wax film, except the stellate trichomes, which also have wax granules. The adaxial surface is glabrous.

Q. affinis **Scheidw.** The abaxial surface has grooved wax film and granules, the adaxial surface has platelets. The stomata are raised and covered with wax film (Fig. 12). On the abaxial surface we observed simple trichomes (29-91 μm) and fasciculate stipitate trichomes with 12 rays (184-324 μm). On the adaxial surface there are simple (94-104 μm) and multiradiate trichomes with 5-11 rays (69-164 μm). The simple trichomes are covered by wax film with a few grooves, the fasciculate stipitate trichomes with wax film, and the multiradiate trichomes with wax film, grooved film, and granules.

Q. castanea **Née.** This species has wax arranged in platelets on the abaxial surface, and wax arranged in crusts and platelets on the adaxial surface. The stomata are raised and covered with wax platelets. The trichomes on the abaxial surface are simple (79-125 μm), fasciculate with about 4 long arms (462-581 μm), and fasciculate stipitate with 7-8 arms (368-526 μm). Simple trichomes are covered with wax film and fasciculate stipitate trichomes with wax platelets. On the adaxial surface there are short fasiculate trichomes with two arms (177-184 μm), covered with wax crusts.

Q. coccolobifolia **Trel.** The epicuticular wax is arranged in platelets on both leaf surfaces. The stomata are raised, and also covered with wax platelets (Fig. 13). The trichomes on the abaxial surface are fasciculate stipitate (with 7-9 rays, 308-392 μm) with wax granules, and simple (82-100 μm) with wax film on the apical and medial regions and platelets on the base. Trichomes are absent on the adaxial surface.

***Q. conspersa* Benth.** Leaves of this species have granules of wax on the abaxial surface and crusts and granules on the adaxial side. Stomata are at the level of the epidermal surface, covered with wax of the layer type. Trichome types present on the abaxial surface are simple (110-170 μm) and stellate with 7-9 arms, covered with wax layers.

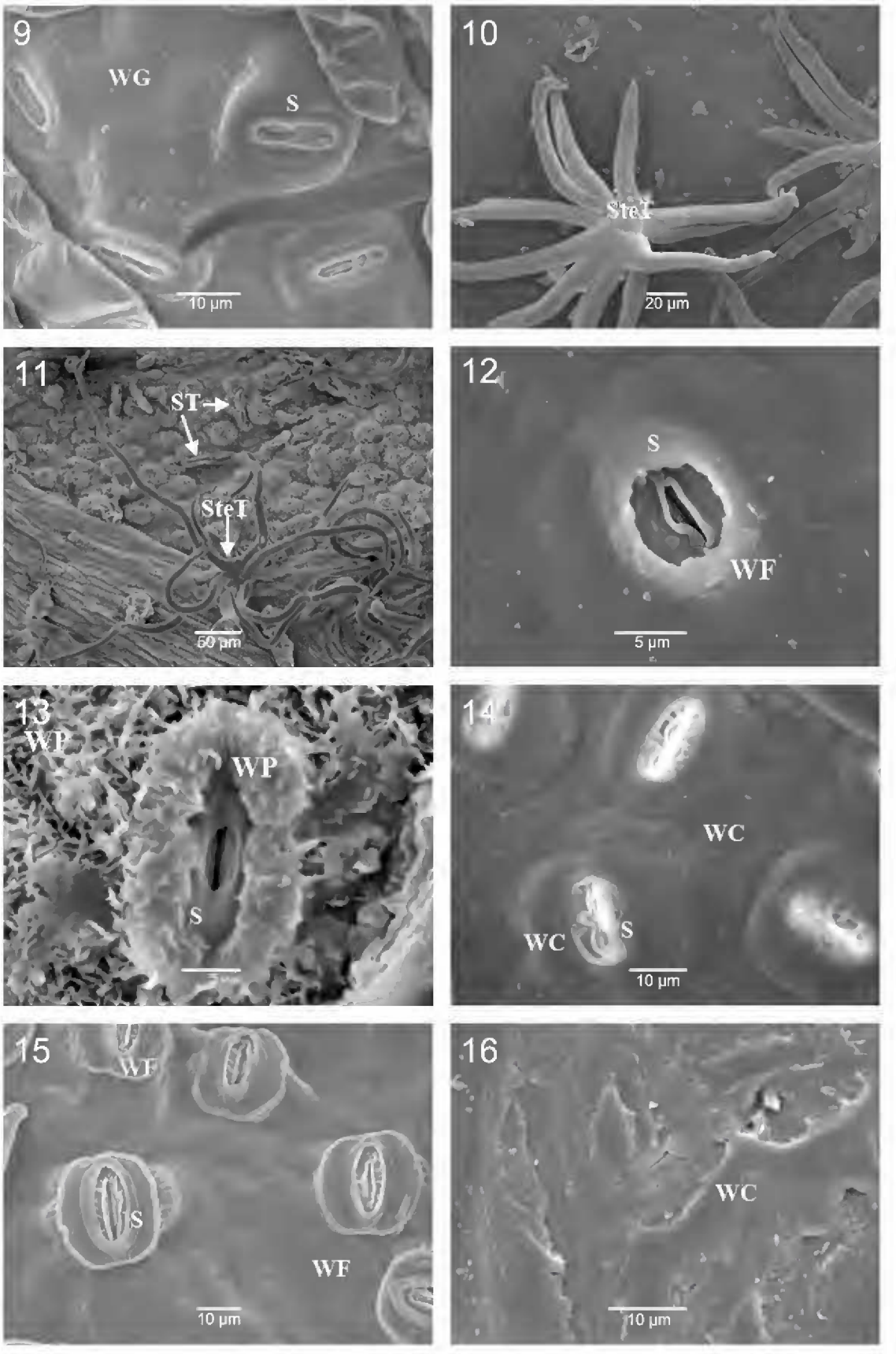
***Q. conzattii* Trel.** Wax crusts are present on both leaf surfaces. The stomata are raised, also with wax crusts (Fig. 14). Trichomes on the abaxial surface are simple (114-183 μm), fasciculate stipitate with 3-8 rays measuring 136-833 μm, and stellate. The wax covering trichomes is of the film-type, with a few grooves. Trichomes on the adaxial surface are simple (74-141 μm) and multiradiate with 6-10 rays (103-184 μm), both types covered with wax films.

***Q. crassifolia* Humb. et Bonpl.** Epicuticular wax films are present on the abaxial surface, and crusts on the adaxial surface. The stomata are raised and covered with wax film. The abaxial surface has simple and fasciculate stipitate trichomes with 8-10 short arms (40-69 μm), and the adaxial surface shows simple trichomes. Film waxes cover all trichomes types in this species.

***Q. crassipes* Humb. et Bonpl.** The abaxial surface is covered by wax film (Fig. 15), while on the adaxial surface waxes are arranged as crusts (Fig. 16) and platelets. The stomata are raised, with wax film (Fig. 15). Simple trichomes (83-139 μm), multiradiate trichomes (9 rays, 77 μm long) and fasciculate stipitate trichomes (5-8 rays, 80-321 μm long) are present on the abaxial surface, all of them covered by wax film. Trichomes were not observed on the adaxial surface.

***Q. crispipilis* Trel.** The abaxial surface is covered with wax film and the adaxial surface with wax crusts. The stomata are leveled with the leaf surface and covered with wax film. The trichome types observed were fasciculate stipitate on the abaxial surface and multiradiate with 6-8 rays (74-100 μm) on the adaxial surface. The wax covering the trichomes is arranged as grooved film.

***Q.* x *dysophylla* Benth.** With epicuticular wax film on both the abaxial and adaxial surfaces. The stomata are raised and also covered with wax film. Trichomes are simple (133-168 μm), fasciculate stipitate (with 5-7 arms, 125-207 μm long) (Fig. 17) and stellate (with 5 arms, 121 μm long) types on the abaxial surface, and of multiradiate type (with 6-8 arms, 78-89 μm long) on the adaxial surface. All trichomes types are covered by wax film (Fig. 18).



Figs. 9-16. (S = stomata, ST = simple trichomes, SteT = stellate trichomes, WC = epicuticular wax crust, WF = epicuticular wax film, WG = epicuticular wax granules, WP = epicuticular wax platelets). Figs. 9, 10. *Quercus resinosa* Liebm. (abaxial and adaxial surface respectively). Fig. 11. *Quercus acutifolia* Née (abaxial surface). Fig. 12. *Quercus affinis* Scheidw. (abaxial surface). Fig. 13. *Quercus coccolobifolia* Trel. (abaxial surface). Fig. 14. *Quercus conzattii* Trel. (abaxial surface). Figs. 15, 16. *Quercus crassipes* Humb. et Bonpl. (abaxial and adaxial surface, respectively).

***Q. eduardii* Trel.** Both abaxial and adaxial surfaces are covered with wax film. The stomata are leveled with the leaf surface and covered with wax film. The abaxial surface has stellate trichomes with 9-15 long rays (72-946 μm) covered with crusts of wax, and simple trichomes (53-112 μm) covered with wax film (Fig. 19). On the adaxial surface there are multiradiate trichomes (with 6-13 rays, 42-243 μm long) and simple trichomes (64-171 μm), both covered with wax film.

***Q. fulva* Liebm.** The abaxial surface has epicuticular wax film and the adaxial surface wax crusts. The stomata are raised and covered with wax crusts. The trichomes observed on the abaxial surface are multiradiate with 12-20 rays (98-180 μm) covered with wax granules, and simple trichomes (150 μm) covered with wax film (Fig. 20), and on the adaxial surface we observed multiradiate trichomes with 9 arms measuring 119-143 μm, covered with wax granules.

***Q. laurina* Humb. et Bonpl.** Epicuticular waxes are of the film type on both surfaces. The stomata are raised and with wax of the film type. On the abaxial surface trichomes are multiradiate with 8 arms (150-160 μm), fasciculate stipitate with 6-11 arms (280-500 μm) and simple (16-265 μm), and on the adaxial surface fasciculate stipitate. Wax film covers all trichome types.

***Q. ocoteifolia* Liebm.** Both leaf surfaces have epicuticular wax film. The stomata are raised and also covered with wax film. The trichomes are stellate, with 4-8 arms (162-368 μm), and simple (78-105 μm) on the abaxial surface (Fig. 21); and stellate with 5-6 arms (267-367 μm), and simple (73-135 μm) on the adaxial surface. All trichomes are covered with grooved wax film.

***Q. radiata* Trel.** Crusts of wax are present on both surfaces. The stomata are both raised above and leveled with the foliar surface and covered with wax crusts. The abaxial surface has simple trichomes (60 μm), multiradiate trichomes with 8 arms (115-156 μm), and fasciculate stipitate trichomes with 6 arms. The trichomes are covered with wax film sometimes approaching granules in shape. The adaxial surface has multiradiate trichomes with 6-8 rays (61-300 μm), covered with wax film.

***Q. scytophylla* Liebm.** Wax crusts are present on both the abaxial and adaxial surfaces. The stomata are raised and also covered with wax crusts. The trichomes on the abaxial surface are multiradiate with 7-8 arms (71-114 μm), covered with wax film. Trichomes were not observed on the adaxial surface.

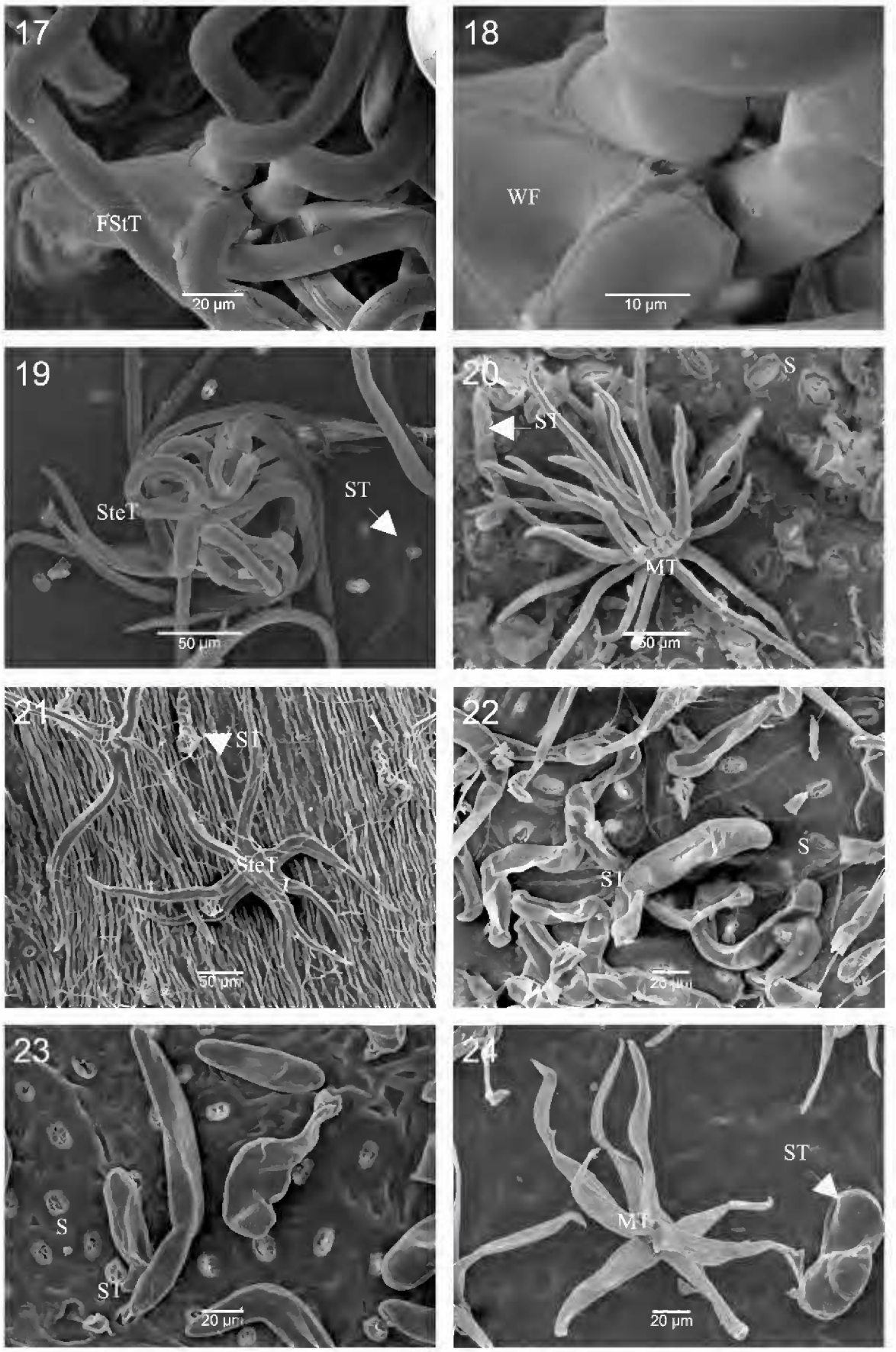
***Q. urbanii* Trel.** Epicuticular wax crusts were observed on both leaf surfaces. The stomata are raised and covered with wax crusts (Fig. 22). The trichomes are simple (103-111 μm) (Fig. 22) and fasciculate stipitate on the abaxial surface; both types covered with wax film. On the adaxial surface there are simple trichomes (93 μm) and fused stellate trichomes with 14 rays (69-100 μm), covered with wax crusts and grooved film, respectively.

***Q. viminea* Trel.** Epicuticular wax films were present on both the abaxial and adaxial surfaces. Stomata are raised and covered with wax film (Fig. 23). The trichome types observed on the abaxial surface were simple (68-173 μm) (Fig. 23), stellate (with 5 rays, 68-87 μm long) and bulbous (15-23 μm), and on the adaxial surface simple (74-102 μm) and multiradiate (with 6-11 rays, 59-150 μm long) (Fig. 24). All the trichome types are covered with grooved wax film.

These results indicated that the five groups of closely related species with some problems of taxonomic delimitation that were included in the study, namely 1) *Q. liebmannii*, *Q. magnoliifolia*, *Q. peduncularis* and *Q. resinosa*, 2) *Q. affinis*, *Q. laurina* and *Q. ocoteifolia*, 3) *Q. conzattii*, *Q. radiata* and *Q. urbanii*, 4) *Q. acutifolia* and *Q. conspersa* and 5) *Q. coccolobifolia* and *Q. viminea*, show qualitative differences in the types of waxes and trichomes present, as well as quantitative differences in the number and length of trichome rays, thus contributing to an important extent to the characterization of these species. This has permitted the elaboration of identification keys to separate the species within each of these groups:

Group 1

1 Adaxial leaf surface glabrous.
  2 Abaxial surface with simple, fasciculate stipitate and fasciculate trichomes, epicuticular wax forming platelets on the abaxial surface and platelets in rosettes on the adaxial surface ..... *Q. peduncularis*
  2 Abaxial surface with simple and fused stellate trichomes, wax film on the abaxial surface and grooved film on the adaxial surface .... *Q. magnoliifolia*
1 Adaxial surface with trichomes.
  3 Trichomes simple on the adaxial surface, abaxial surface with stellate, fused stellate and fasciculate stipitate trichomes, wax forming films on the abaxial surface and crusts on the adaxial surface ..... *Q. liebmannii*
  3 Trichomes multiradiate and stellate on the adaxial surface, abaxial surface with simple, fused stellate and fasciculate stipitate trichomes, wax forming films on the adaxial surface and granules on the abaxial surface .... *Q. resinosa*



Figs. 17-24. (FStT = fasciculate stipitate trichomes, MT = multiradiate trichomes, S = stomata, ST = simple trichomes, SteT = stellate trichomes, WF = epicuticular wax film). Figs. 17, 18. *Quercus dysophylla* Benth. (abaxial surface). Fig.19. *Quercus eduardii* Trel. (abaxial surface). Fig. 20. *Quercus fulva* Liebm. (abaxial surface). Fig. 21. *Quercus ocoteifolia* Liebm. (abaxial surface). Fig. 22. *Quercus urbanii* Trel. (abaxial surface). Figs. 23, 24. *Quercus viminea* Trel. (abaxial and adaxial surface, respectively).

Group 2

1 Trichomes stellate on both the adaxial and abaxial surfaces..... *Q. ocoteifolia*

1 Trichomes multiradiate and fasciculate stipitate on one or both surfaces.

2 Trichomes simple and multiradiate on the adaxial surface, abaxial surface with fasciculate stipitate trichomes, epicuticular wax forming platelets on the adaxial surface and grooved films and granules on the abaxial surface .... *Q. affinis*

2 Trichomes fasciculate stipitate on the adaxial surface, abaxial surface with simple, multiradiate and fasciculate stipitate trichomes, wax forming films on both surfaces ..... *Q. laurina*

Group 3

1 Trichomes simple and fused stellate on the adaxial surface, abaxial surface with simple and fasciculate stipitate trichomes, multiradiate trichomes absent .... *Q. urbanii*

1 Trichomes multiradiate on the adaxial or both surfaces.

2 Trichomes multiradiate on the adaxial surface, abaxial surface with simple, multiradiate and fasciculate trichomes ..... *Q. radiata*

2 Trichomes simple and multiradiate on the adaxial surface, abaxial surface with simple, stellate and fasciculate stipitate trichomes on the abaxial surface ..... *Q. conzattii*

Group 4

1 Adaxial surface glabrous, abaxial surface with simple, solitary, multiradiate and stellate trichomes, wax forming films, crusts and platelets on the adaxial surface and crusts, granules and platelets on the abaxial surface ..... *Q. acutifolia*

1 Adaxial surface glabrous, adaxial surface with simple and stellate trichomes, wax forming crusts and granules on the adaxial surface, and granules on the abaxial surface ..... *Q. conspersa*

Group 5

1 Adaxial surface glabrous, abaxial surface with simple and fasciculate stipitate trichomes, wax forming platelets on both surfaces ..... *Q. coccolobifolia*

1 Adaxial surface with simple and multiradiate trichomes, abaxial surface with simple, bulbous and stellate trichomes, wax forming films on both surfaces .... *Q. viminea*

DISCUSSION

The variation observed among Mexican oak species in all micromorphological features examined confirmed the high taxonomic value of these foliar characters, particularly epicuticular waxes and trichomes. The combination of character states was different for each species, thus making it possible to use these features to differentiate even those species that are difficult to distinguish on the basis of macromorphological characters only. However, at higher taxonomical levels few clearly distinctive traits could be found among the different groups. In previous studies, Hardin (1979a, b) suggested that certain trichome types are characteristic for particular groups of oak species in Eastern North America. For example, he found that stellate trichomes were restricted to section *Quercus* (white oaks) and that the fused stellate type was only present in the *Virentes* group ("live oaks"). Additionally, rosulate and multiradiate trichomes were only observed in section *Lobatae* (red oaks) (Hardin, 1979a, b). In the case of European species, Llamas et al. (1995) observed fused stellate trichomes in *Sclerophyllodrys* and *Cerris* species, and solitary, multiradiate and stellate trichomes in white oak species. Bussotti and Grossoni (1997) reported stellate and fused stellate trichomes in *Sclerophyllodrys*, the stellate and multiradiate types in *Cerris*, and for section *Quercus*, mainly the stellate and fasciculate stipitate types. In our study, multiradiate trichomes were not observed in white oaks with the exception of *Q. resinosa*, while 67% of the red oak species had this type of trichome (Table 2). The fused stellate type was present in *Q. oleoides* (*Virentes* group), but also in four other white oak species, and absent in red oak species, except *Q. urbanii*. The frequency of presence of the other trichome types did not differ very markedly between red and white oaks (Table 2). These patterns indicate that parallel losses and acquisitions of trichome types have occurred among the individual species and species groups in the genus *Quercus* (Hardin, 1979b).

Fewer studies have examined the variation in epicuticular waxes among oak species. Bussotti and Grossoni (1997) found that the abaxial surface of European white oaks is characterized by waxes arranged in vertical scales, and *Cerris* and *Sclerophyllodrys* by smooth waxes. A comparatively wider diversity of waxes was observed in the Mexican oaks, although species groups were not clearly characterized by specific types (Table 3).

The examination of trichome traits has also been considered to serve as a reliable clue to identify hybridization among oak species, because the trichomes of some putative hybrids appear to be a combination of the parental types (e.g. Hardin, 1979b; Spellenberg, 1998). The samples analyzed in this study included a hybrid

taxon, *Q.* x *dysophylla* and its two putative parental species, *Q. crassipes* and *Q. crassifolia* (Tovar-Sánchez and Oyama, 2004). In this case, a clear pattern of combination of the parental traits in the hybrid was not observed. The hybrid had traits not observed in any of the putative parental species (stellate trichomes), and lacked other traits present in both parents (epicuticular wax crusts) (Tables 2 and 3). This result shows, as has been emphasized in several recent studies and reviews (McDade, 1990; Rieseberg and Ellstrand, 1993; Rieseberg et al., 1999), that the non-intermediacy of phenotypic characters can occur in hybrids, which instead are most often a mosaic of characters states that can be identical to one parent, intermediate, more extreme than the parental states, or novel. Therefore, the unambiguous determination of hybrids on the sole basis of morphological characters can be problematical, and the use of genetic markers is recommended (Tovar-Sánchez and Oyama, 2004).

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